

## CLIMATE CHANGE AND GRASSLAND RESTORATION IN CALIFORNIA: LESSONS FROM SIX YEARS OF RAINFALL MANIPULATION IN A NORTH COAST GRASSLAND

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### ABSTRACT

Native perennial bunchgrasses have undergone steep declines across much of California but persist in sizable populations along the northern coast. The longer rainy season and less severe summer drought in this region are thought to facilitate bunchgrass persistence in the face of extensive invasion by exotic annual species. Changes in the seasonality and intensity of precipitation that accompany global climate change could critically influence efforts to conserve and restore these plants in California grasslands. We established a large-scale manipulation of rainfall in a protected Mendocino County grassland to investigate how predicted shifts in precipitation affect the performance of three native perennial bunchgrass species in exotic-dominated stands. We added seeds, plugs, and mature tussocks of *Danthonia californica*, *Elymus glaucus*, and *Elymus multisetus* into replicate plots of exotic annual grassland and subjected the plots to one of three experimental precipitation regimes: increased winter rainfall, increased spring rainfall, and ambient rainfall. Responses to rainfall addition varied widely by age class and species and depended heavily on seasonal timing of the increase. Establishment from seed was rare for all three species and showed little response to water addition, likely due to concomitant changes in the surrounding communities. Production of exotic annual grasses rose markedly following repeated extensions of the rainy season, and while established bunchgrasses benefited despite this change, new plants could not establish into thickening stands of exotic vegetation. In contrast, survival was high for transplanted plugs and tussocks of all three species across all three rainfall treatments, suggesting that plugs and tussocks can survive a wide range of climatic conditions and high local densities of exotic annual grasses. Restoration approaches focused on these life stages may be most robust to changing climate. Transplanted individuals can provide a continual source of propagules to surrounding areas that then recruit during years in which conditions in the physical and biological environment are amenable to seedling establishment.

**Key Words:** bunchgrasses, *Danthonia californica*, ecological restoration, *Elymus glaucus*, *Elymus multisetus*, perennial grass, precipitation.

Restoration of native plants in exotic-dominated grasslands is a major conservation challenge in California. Annual grass and forb species from Europe and Asia dominate most grasslands, with native perennial grass populations sparse across much of the state (Bartolome et al. 1986; Huenneke 1989; Hamilton 1997). Sizeable populations that do remain are generally restricted to northern coastal prairie sites, but even here native plants exist amid abundant exotic cover (Hektner and Foin 1977; Hayes and Holl 2003). Where native perennial bunchgrasses are abundant, they can improve summer grazing (Wagner 1989), increase ecosystem nutrient retention (Menke 1989; Adams et al. 1999), and restrict further invasion by exotic species (Peart 1989a; Corbin and D'Antonio 2004a). Conservation efforts

therefore seek to establish or maintain native bunchgrass populations in the face of extensive invasion by exotic species.

Scientists and managers have evaluated techniques such as fire, grazing, and carbon addition for their ability to improve the establishment and performance of native grasses (e.g., Hatch et al. 1999; Corbin and D'Antonio 2004b; Corbin et al. 2004). Ultimately, however, the effectiveness of any management practice could be strongly influenced by climate. Extended drought in the nineteenth century is thought to have played an important role in the widespread replacement of California's native perennial grasses by exotic annual species (Major 1988; Mack 1989), and the success of native bunchgrasses along the northern coast likely stems in part from the longer winter rainy seasons and shorter summer droughts that characterize the region (Elliot and Wehausen 1974; Heady et al. 1977, 1992; Peart 1989b; Stromberg et al. 2001). Changes in precipitation

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regimes that accompany global climate change could have pronounced effects on native perennial bunchgrasses.

General circulation models developed at both the *Hadley Centre for Climate Prediction and Research* (HadCM2) and the *Canadian Centre for Climate Modeling and Analysis* (GCCM1) forecast substantial increases in precipitation throughout northern California over the next century (National Assessment Synthesis Team 2000). The two models differ, however, in the predicted seasonality of these increases. In this difference may lie considerable implications for the future of California's grasslands.

The *Hadley* model calls for the entirety of the precipitation increase to fall within California's current winter rainy season, with no effect on the length or severity of annual summer drought. Rainfall during the winter and early spring in northern California generally exceeds the amount necessary for plant growth (Pitt and Heady 1978), so winter-time increases may be largely superfluous. Effects could manifest if increased winter rainfall eliminates the mid-winter dry spells typical in northern California. Every winter rainy season in the last fifty-six years in northern California has experienced a rain-free period of at least eight and on average nineteen consecutive days (Null 2006). Established bunchgrasses have slow winter growth rates and deep root systems that buffer them from the short-term drying of surface soils that can accompany these dry spells (Holmes and Rice 1996; Reever Morgan et al. 2007), but shallowly-rooted grass seedlings can be negatively impacted (Bartolome 1979; George et al. 1985; Young and Evans 1989). Increased winter rainfall could then potentially benefit newly germinated perennial grass seedlings, but net effects would depend on the relative benefit to these plants versus their annual competitors.

The *Canadian* model projects increased rainfall extending into the spring and summer. This could have more pronounced effect on perennial bunchgrasses. California grassland communities are strongly affected by the state's Mediterranean climate, in which 95% of annual precipitation typically falls between the months of November and April (Major 1988). Late spring and summer rainfall is typically rare, but when it does occur it can increase productivity, extend the period of activity, and improve autumn regrowth of native bunchgrasses (Laude 1953; Jackson and Roy 1986). In contrast, exotic annual grasses in California maximize their productivity and reproduction at the time of high water availability in spring, senesce by mid-May, and are generally unresponsive to extensions of the rainy season beyond April (Pitt and Heady 1978; Jackson and Roy 1986). This strategy is well suited to the current climate, but would not allow exotic annuals much direct benefit from increased

spring and summer rainfall associated with global change. Previous work in our study system, however, has shown that exotic annual species can benefit indirectly from extension of the rainy season via a fertilization effect caused by increased productivity and extended seasonal activity of nitrogen-fixing legumes (Suttle et al. 2007). Net effects, again, may then depend on the relative magnitude of native bunchgrass benefit versus the increased competition they could experience from stimulated annual grass productivity.

We manipulated rainfall over large plots of exotic-dominated grassland for six years to explore potential consequences of each scenario for individual- and population-level performance of three native perennial bunchgrasses.

## METHODS

*Study System.* The study was conducted at the Angelo Coast Range Reserve in Mendocino County, California (39°43'45"N, 123°38'40"W). Grasslands at this site occur on abandoned terraces of the South Fork Eel River, with soils derived from rocky mudflows across terrace surfaces. Vegetation is a well-mixed assemblage of annual and perennial grasses and forbs of both native and exotic origin. Mean annual precipitation is 216 cm (P. Steel, University of California Natural Reserve System unpublished), with the vast majority falling between the months of November and March. Local topography blocks coastal fog, so summers are hotter and drier at the study site than along the nearby coast (Johnson 1979).

*Experimental Design.* The experiment consisted of eighteen circular plots, each nearly 70 m<sup>2</sup>, subjected to one of three watering treatments in a randomized design (Fig. 1). Treatments included a winter addition of water (January through March) simulating an intensification of the rainy season, a spring addition of water (April through June) simulating an extension of the rainy season, and a control in which no water was added above ambient rainfall.

Water diverted from a mountain spring and filtered to 40 microns was delivered to experimental plots using sprinklers designed to distribute water evenly over circular plots (Rain Bird® Rain Curtain™, Azusa, CA). Inorganic nitrogen concentrations in the water fall within the natural range of concentrations in ambient rainfall at the study site. The water delivery protocol was identical for the winter and spring addition treatments—valves leading to the sprinklers were actuated by battery-operated timers set to "rain" 14 to 16 mm of water on the plots approximately two hours after dawn every third day for 87 d, regardless of ambient weather. Each watered plot

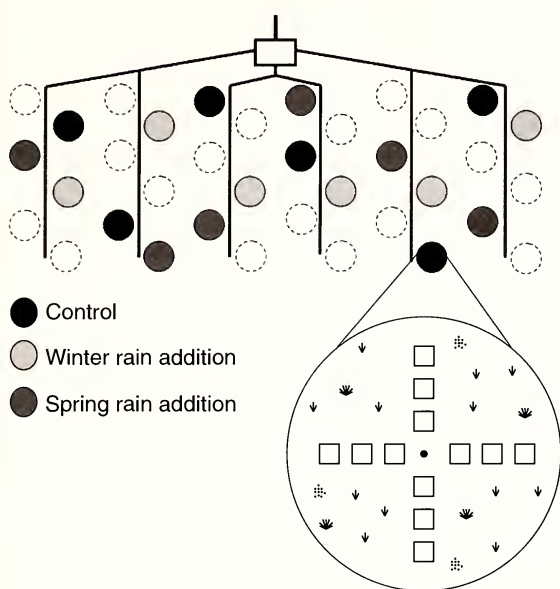


FIG. 1. Schematic of experimental design, illustrating assignment of treatments across plots and seed, plug, and tussock additions within a plot. Seeds, plugs, and tussocks were added to experimental plots at least 0.5 m away from the twelve permanent subplots used to monitor natural recruitment of native grasses. Experimental plots were approximately 70 m<sup>2</sup> and were separated from neighboring plots by at least 5 m. Solid lines show the layout of the buried irrigation system; circles with dotted outlines indicate plots used in separate research.

received approximately 44 cm of supplementary water per year, representing roughly a 20% increase over the long-term mean.

We examined effects of seasonal watering over six years on three native perennial C<sub>3</sub> grasses: *Danthonia californica*, *Elymus glaucus*, and *Elymus multisetus* (nomenclature follows Hickman 1993). All three species are widely distributed across western North America, common components of remnant and restored native grasslands, and ecologically significant in coastal prairie; *Danthonia* is considered diagnostic for the type (Heady et al. 1977). Although the three species we chose to focus on occur in close proximity within our field site, they are known to differ in their habitat associations across larger spatial scales. *Danthonia* is categorized as a facultative wetland species while the two *Elymus* taxa are not (USDA NRCS 2007). *Elymus glaucus* is often found in moderately mesic woodland and grassland sites, while *E. multisetus* is most common in drier habitats with sandy or rocky soils (Hickman et al. 1993). All three species are abundant along the edge of the study meadow but were absent from most experimental plots when the experiment was laid out. Prior to beginning the manipulation, we designated twelve permanent subplots (50 cm × 50 cm) within each plot in which to monitor

natural bunchgrass recruitment across the study. We then added *Danthonia*, *E. glaucus*, and *E. multisetus* to each experimental plot as seed, “plugs” (plants of 2–3 cm basal diameter), and “tussocks” (plants of approximately 10 cm basal diameter) at least 50 cm outside of the “recruitment” subplots (Fig. 1).

Plugs and tussocks were harvested from outside experimental plots by stabbing the flat blade of an OST® Tree Planter vertically in a square pattern around each plant to 25 cm depth and prying the soil block upward. These were then transplanted into experimental plots. The size and planting method used for plugs make them approximations of the individuals grown for use in restoration projects, but ours were likely older. Transplanting large tussocks may not be a viable restoration approach at large spatial scales, but could be used in small areas to overcome local propagule limitation (Sheley and Krueger-Mangold 2003), a potential problem in some California grassland sites (Hamilton et al. 1999; Seabloom et al. 2003a).

We transplanted four plugs of each species into experimental plots in December 2000, capitalizing on conditions of high soil moisture. We monitored survival of these plants annually until March 2005, at which time we measured the basal diameter of tussock vegetation for comparison of plant sizes across watering treatments. Tussock vegetation was bunched tightly in hand immediately above the ground surface, and digital calipers were fitted around the tight vegetative bunch.

In August 2001, we sowed seeds of each species into separate 25-cm × 25-cm areas of intact vegetation or disturbed bare soil within each experimental plot. For each seed addition, we added 50 seeds collected from seed heads of plants at the study site. For *D. californica*, we also added five basal culm sections, because this species produces cleistogamous florets in its flowering culm bases in addition to distal seeds. DiVittorio et al. (2007) measured mean native perennial grass seed rain of 620 seeds m<sup>-2</sup> (range = 0–2200) across a gradient of native perennial grass cover in another northern California coastal prairie site, so our seed densities (800 seeds m<sup>-2</sup>) are consistent with natural inputs. Subplots were surveyed for seedling establishment during the following summer. We repeated seed additions in new areas within each plot in August 2003 and surveyed these in summer 2004.

In December 2001, we transplanted mature *E. glaucus* and *D. californica* tussocks into experimental plots. *Elymus multisetus* was initially excluded owing to concerns over its scarcity in the meadow, but following large recruitment in 2001 and 2002, we transplanted a mature tussock of this species in December 2002. We measured tussock reproductive output by counting the



TABLE 1. TOTAL NUMBER OF SEEDLINGS OF THREE NATIVE GRASS SPECIES THAT ESTABLISHED IN RESPONSE TO SEED ADDITION ONTO 25-cm BY 25-cm STANDS OF INTACT VEGETATION AND DISTURBED SOIL ACROSS ALL WATERING TREATMENT PLOTS IN 2002 AND 2004.

	Species	Control		Winter +		Spring +	
		Vegetation	Soil	Vegetation	Soil	Vegetation	Soil
2002	<i>Danthonia</i>	0	0	0	0	1	1
	<i>E. glaucus</i>	0	0	0	0	3	2
	<i>E. multisetus</i>	1	na	3	na	3	na
2004	<i>Danthonia</i>	1	1	2	2	0	4
	<i>E. glaucus</i>	0	0	0	1	0	4
	<i>E. multisetus</i>	2	na	3	na	1	na

flowering culms produced each summer. We measured leaf carbon dioxide and water vapor exchange rates of planted tussocks using a LI-6400 portable photosynthesis system (LI-COR, Lincoln, NE) in early June 2003. *Danthonia californica* and *E. glaucus* tussocks were sampled in all plots, but *E. multisetus* had senesced by this date in one ambient and one spring-watered plot, so only 16 individuals were measured. Measurements were taken within two hours of solar noon on two consecutive sunny days. Chamber conditions were set to 400 ppm CO<sub>2</sub>, 1000 μmol/m<sup>2</sup>/s photosynthetically active radiation, 25°C, and ambient humidity. Sampled leaf portions were collected and their areas determined using a LI-3100C leaf area meter (LI-COR, Lincoln, NE). Leaf area values were used to correct gas exchange values and calculate per leaf area photosynthetic rate and water use efficiency (WUE) for each individual.

Finally, we counted native bunchgrasses in all permanent subplots inside each plot in January 2007 to assess how the different rainfall regimes had impacted the recruitment of new plants into stands of exotic-dominated vegetation over the previous six years.

**Statistical Analyses.** The rarity of establishment from seed for any of the three species precluded statistical testing for effects of watering treatment within a single species or for differences in establishment between intact vegetation and disturbed soil. We tested for watering treatment effects on survival, growth, reproductive output, photosynthetic rate and WUE of each species separately, using one-way ANOVA, followed by Tukey tests when significant treatment effects were detected. We conducted the ANOVA of plug size in 2005 on plot-wide means for all surviving plants of each species, having eliminated from the analysis plots with no surviving plugs for a given species. Proportional plug survival data were arcsine-square root transformed and tussock culm production data were square root transformed prior to analysis to meet assumptions of normality and equality of variances. We tested for time by treatment interactions in flowering

culm production across years with repeated measures ANOVA. After this analysis revealed no significant time by treatment interactions ( $P >> 0.10$ ), we condensed reproductive data by calculating average culm production for each plant across all years of measurement.

RESULTS

**Seed and plug additions.** Seedling establishment was rare following either year of seed addition: a total of fourteen and twenty-one seedlings established in 2002 and 2004, respectively (see Table 1 for treatment and species totals). Across both years, five seedlings established in ambient rainfall plots, eleven in winter water addition plots, and nineteen in spring-watered plots.

Spring water addition more than doubled the survival of the four *D. californica* plugs planted per plot relative to winter-addition and ambient conditions ( $F_{2,15} = 11.03$ ,  $P < 0.01$ ) (Fig. 2). There was a nearly-significant increase in *E. glaucus* survival in spring-watered plots ( $F_{2,15} = 3.64$ ,  $P = 0.052$ ), but no effect of watering treatment on *E. multisetus* ( $F_{2,15} = 0.57$ ,  $P > 0.10$ ).

Treatment effects on vegetative growth of plugs were likewise apparent for only two of the three species. *Danthonia californica* plants grew approximately twice as large in spring-addition plots as in winter-addition or control plots ( $F_{2,15} = 13.81$ ,  $P < 0.001$ ), while *E. glaucus* plugs were more than three times larger in winter and spring water addition plots than in ambient control plots ( $F_{2,15} = 9.72$ ,  $P < 0.01$ ; Fig. 2). *Elymus multisetus* growth did not respond to watering treatment ( $F_{2,15} = 1.71$ ,  $P > 0.1$ ).

**Reproductive output and physiology of mature tussocks.** All mature tussocks transplanted into plots survived through the duration of the experiment. Spring water addition increased production of flowering culms in both *D. californica* ( $F_{2,15} = 6.34$ ,  $P = 0.01$ ) and *E. glaucus* ( $F_{2,15} = 11.24$ ,  $P < 0.01$ ) relative to winter addition and control conditions (Fig. 2). Both species pro-

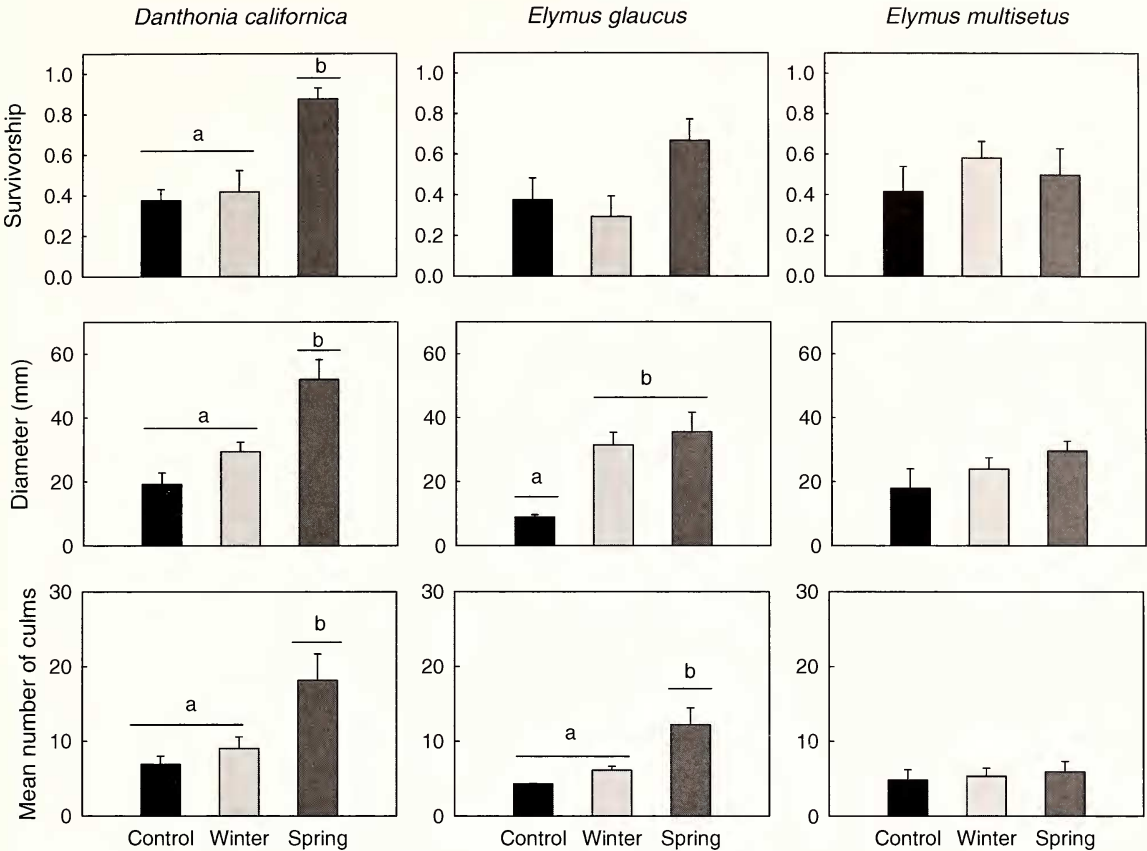


FIG. 2. Watering treatment effects on the proportional survivorship and growth of plugs and the mean reproductive output of mature tussocks of three native grass species across five years of rainfall manipulation. Letters indicate statistically significant differences between treatment groups revealed in *post hoc* Tukey tests.

duced about twice as many culms when receiving additional spring rainfall than under winter-addition or ambient rainfall conditions. There was again no response from *E. multisetus* ( $F_{2,15} = 0.24$ ,  $P > 0.1$ ).

Watering treatment had a significant effect on photosynthetic rates of all three species (*D. californica*  $F_{2,15} = 7.63$ ,  $P < 0.01$ ; *E. glaucus*  $F_{2,15} = 3.69$ ,  $P < 0.05$ ; *E. multisetus* ( $F_{2,13} = 5.22$ ,  $P < 0.05$ ; Fig. 3). Spring water addition increased *D. californica* carbon gain per unit leaf area by more than 70% relative to ambient or winter water addition conditions. In contrast, *E. multisetus* individuals in winter addition plots had approximately 40% lower photosynthetic rates than those in ambient or spring water addition plots. Photosynthesis of *E. glaucus* individuals across watering treatments did not differ significantly in *post hoc* tests.

Water use efficiency varied significantly with watering treatment for both *Elymus* species (*E. glaucus*  $F_{2,15} = 8.36$ ,  $P < 0.01$ ; *E. multisetus*  $F_{2,13} = 5.20$ ,  $P < 0.05$ ; Fig. 4) but not for *D. californica* ( $F_{2,15} = 1.95$ ,  $P > 0.10$ ). The average WUE of *E. glaucus* plants in ambient and winter

water addition plots was greater than that of individuals in spring-watered plots (7.1 vs. 3.9 mmol C mol  $H_2O^{-1}$ ). For *E. multisetus* individuals, the WUE of individuals experiencing ambient conditions was intermediate (5.3 mmol C mol  $H_2O^{-1}$ ) between those in winter- and spring-watered plots (7.4 and 4.6 mmol C mol  $H_2O^{-1}$ , respectively).

**Population-level recruitment.** Over six years, natural recruitment of new plants into exotic-dominated stands was low across species and absent altogether for *Elymus glaucus*. *Danthonia californica* and *Elymus multisetus* did revegetate portions of the grassland, but not in a manner that varied with watering treatment. Across the twenty-four experimental plots in which native grasses accounted for <5% of ground cover at experiment's start (including plots not included in the research described here—see Fig. 1), mean recruitment was actually highest in control plots (Fig. 4), although highly variable and with no significant difference among treatments. An average of  $3.5 \pm 1.7$  (mean  $\pm 1$  SE) new bunchgrass recruited into the 3 m<sup>2</sup> of vegetation (12 subplots  $\times$  0.25 m<sup>2</sup> each) monitored in each

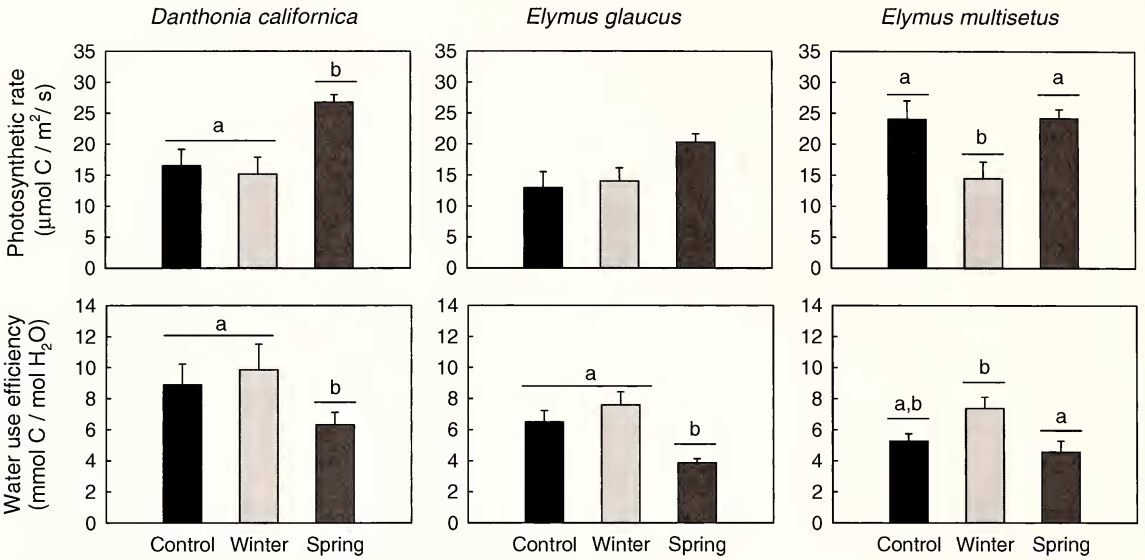


FIG. 3. Effect of watering treatment on tussock photosynthetic rate and water use efficiency in June 2003, two months after the end of winter water addition and the beginning of the spring watering treatment. Letters indicate statistically significant differences between treatment groups revealed in *post hoc* Tukey tests.

control plot, with  $1.1 \pm 0.6$  new plants in winter-addition and  $2.9 \pm 1.0$  new plants in spring-addition plots.

*Exotic annual grasses.* Effects of water addition on other plant species and on higher trophic levels are described in detail elsewhere (Suttle et al. 2007). It is noteworthy here to state that the favorable responses to spring water addition by established *Danthonia* and *Elymus glaucus* plants occurred alongside marked increases in the production of exotic annual grass species such as *Bromus hordeaceus* and *B. diandrus*. These annual

grasses showed little direct response to water addition, occurring at similar biomass across all three treatments through the first year of the experiment. In subsequent growing seasons, however, they appeared to benefit strongly from a fertilization effect driven by the nitrogen-fixing *Lotus micranthus*. Following dramatically increased production and extended longevity of this legume in spring-watered plots in one year, annual grass production and tissue nitrogen concentrations rose markedly in the next. As this cycle was repeated again and again, annual grass biomass in spring-addition plots came to more than double that in control and winter-addition plots in some years (Suttle et al. 2007).

DISCUSSION

Information on how climate change will impact species and habitats is urgently needed, both to improve our understanding of specific threats and to guide allocation of limited conservation resources in addressing them. In California, changes in precipitation regimes that accompany global climate change could have profound consequences for grassland structure and species composition, but with impacts varying by species and life stage, tied strongly to seasonal timing, and propagating widely through interaction webs, reliable predictions of these consequences will be difficult to attain. Predictions based on generalized life history differences between native and exotic plants are clearly insufficient. This prudence gains further support as perceptions change over the original native composition of these systems, with re-

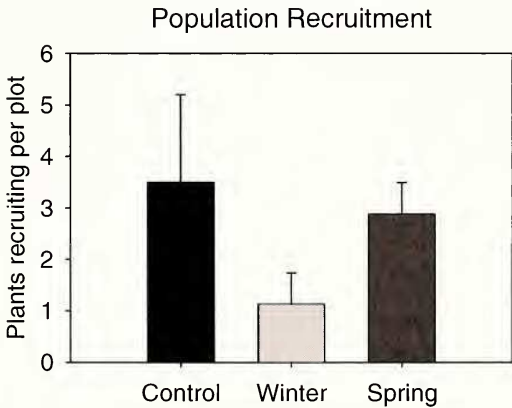


FIG. 4. Effect of watering treatment on population-level recruitment by native grasses into experimental plots over six years of rainfall manipulation. Data represent mean  $\pm$  SE) number of new individual bunchgrasses recruiting into the permanent subplots arrayed through each experimental plot between 2001 and 2007.



searchers coming to appreciate that annual forbs were important original components of California's grassland landscapes (Jepson 1925; Hamilton 1997—see Seabloom et al. 2003b for a study of native forb restoration). The native perennial/exotic annual dichotomy is made more obsolete as exotic perennial bunchgrasses such as *Holcus lanatus* and *Anthoxanthum odoratum* become increasingly abundant along California's northern coast. Through other work in this study system, we have found that increased spring water availability strongly favors establishment and survival of *Holcus lanatus* and could facilitate its spread into new areas (Thomsen et al. 2006).

Many authors have already commented that geographic origin alone is not a biologically significant characteristic, making it unwise to expect native versus exotic species to exhibit consistent responses to the environment and to other species (e.g., Levine and D'Antonio 1999; Davis et al. 2001). Similarly, several California researchers have argued against the tendency to treat *Nassella pulchra*, a prominent focus of California grassland research and restoration efforts, as broadly representative of the state's native bunchgrasses (Huntsinger et al. 1996; Hamilton 1997; Hatch et al. 1999). Our results support this call for caution when generalizing across California's perennial bunchgrass species, demonstrating that these may respond in disparate ways to changing precipitation regimes.

As predicted by life history characteristics, spring watering increased the survivorship, growth, and reproductive output of *D. californica* and *E. glaucus*. In contrast, winter water addition had little effect on any measure of their performance, including seedling establishment, which we predicted might be positively influenced by amelioration of mid-winter dry spells. *Elymus multisetus*, meanwhile, showed no response to either watering treatment in any measured response. Adaptations that allow *E. multisetus* to survive in extremely dry conditions may be present at the expense of those that would allow favorable responses to unusually high moisture levels.

Our measurements of summertime plant physiology provide some insight into these differing responses. *Danthonia* and *E. glaucus* had higher photosynthetic rates and lower water use efficiencies in spring-addition plots than under ambient and winter-addition treatments. Thus spring water addition, as expected, extends the active growing season for these species. In contrast, *E. multisetus* tussocks had comparably high photosynthetic rates in control and spring-addition plots, and significantly lower carbon gain in winter-addition plots. Water use efficiency followed a complementary pattern, with greater efficiency in winter-addition plots than in control or spring-addition plots. Further research is needed to determine the specific mechanisms

underlying these differing responses to water availability.

In general, however, once established in experimental plots all three species fared well regardless of treatment conditions. For transplanted plugs, at least some individuals of every species survived in nearly every plot. These survival rates are high relative to studies that followed young native grass recruits from seed in exotic-dominated grasslands (Dyer et al. 1996; Dyer and Rice 1997; Hamilton et al. 1999; Brown and Rice 2000), presumably because the 2–3 cm diameter plants we harvested for transplant were older. Corbin and D'Antonio (2004a) found that three-month-old native grass seedlings survived well when transplanted into dense plots of exotic annual grasses, supporting the finding here that plugs may be a more effective restoration technique for native grasses than seed additions. Furthermore, the 100% survival of large tussocks that we transplanted into experimental plots agrees with previous work showing that mature natives compete well in exotic-dominated California grasslands (Peart 1989a; Corbin and D'Antonio 2004a).

The strong performance of established individuals may not translate clearly to improved population-level performance, however. Establishment following seed addition was rare across all treatment conditions, in line with previous research showing native California bunchgrasses to be most vulnerable at the seedling stage to competition from surrounding plants (Peart 1989b; Dyer et al. 1996; Dyer and Rice 1997; Hamilton et al. 1999; Brown and Rice 2000; Corbin and D'Antonio 2004a,b), and recruitment from seed to be low even where sizeable bunchgrass populations exist (Bartolome and Gemill 1981; Peart 1989b). We measured seedling establishment after only two years of seed addition, but across the full six-year experiment both *Danthonia* and *Elymus multisetus* seedlings have begun to appear in plots from which they were absent at experiment's start (K. B. Suttle personal observation).

Seedling recruitment will be heavily influenced by the specific climate and surrounding plant assemblage each year, and the interactive effects of these factors warrant further study. Established bunchgrasses, on the other hand, can persist through a wide range of climatic conditions and competitive environments, seeding the surrounding area with propagules over many years or decades. Revegetation of exotic-dominated stands via recruitment from these propagules may proceed slowly, but given the high interannual variability in climate and grassland standing crop and species composition characteristic of California, sporadic bursts of revegetation can be expected. Restoration approaches that focus on individual transplants should thus be fairly robust

to environmental change. Given the complexities of climatic and ecological prediction, maximizing robustness of restoration measures to a wide range of conditions should be a foremost goal.

#### ACKNOWLEDGMENTS

We thank J. Miner, J. Bastow, C. McNeely, and T. Popp for assistance in the field; M. Power and C. D'Antonio for support and discussion; J. Abraham, J. Corbin, R. Evett, M. Vasey, and an anonymous reviewer for constructive comments on the study; J. Corbin and participants in the 2006 Society for Conservation Biology symposium "Ecological restoration in a changing world: Case studies from California" for critical insights and discussion; and P. Steel and the University of California Natural Reserve System for protection and stewardship of the study site. This work was supported by a Canon National Parks Science Scholarship and an EPA STAR Fellowship to KBS, an NSF Graduate Research Fellowship to MAT, and the California Native Plant Society.

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